

COMPARISON OF AUTUMN AND WINTER DEVELOPMENT OF TWO WOLF SPIDER SPECIES (*PARDOSA*, LYCOSIDAE, ARANEAE) HAVING DIFFERENT LIFE HISTORY PATTERNS

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ABSTRACT. *Pardosa* species do not overwinter in the adult stage in the Holarctic region, therefore penultimate instars should avoid precocious maturation in autumn. We tested how artificially increased temperature and/or lengthened light regime would affect the pre-overwintering development of two common species with different phenological patterns. Juvenile instars of *Pardosa agrestis* (Westring 1861) and *P. hortensis* (Thorell 1872) were collected in autumn from the field. The experimental spiders were held either indoor at 26 °C or outdoors at ambient temperature and were exposed either to short or to long daylength. Molting events were monitored for five months. At outdoor temperatures no spiders reached adulthood and molts of younger instars occurred more frequently at long daylength. In the indoor temperature groups all *P. hortensis* and the majority of *P. agrestis* individuals reached adulthood during the experiment. Long daylength treatment enhanced the effect of increased temperature by almost halving the time needed to reach adulthood in both species. Penultimate instars of both species needed at least 17 days to molt, while earlier instars, present only in *P. agrestis*, responded rapidly to higher temperature by molting. This stage dependent response suggests that earlier instars can use favorable autumnal temperatures to catch up with penultimate instars which leads to higher synchrony of developmental stages in the overwintering and spring populations.

Keywords: Life history, overwintering, diapause, stenochronous, wolf spider

Pardosa species reach high population densities in a number of habitat types, including agricultural habitats, all over the world. In the Holarctic region most of the species are stenochronous with spring–summer reproduction, overwintering as immature instars. However, some species have a rather flexible life history pattern—being biennial, annual–biennial or having a one year life cycle depending on latitude (Edgar 1972; Stepczak 1975) or the primary productivity of the habitat (Schmoller 1970). There are also indications that certain species may have two generations per year in more southern latitudes (Miyashita 1969; Samu et al. 1998). In spite of this flexibility in life history pattern and the significant winter activity observed in some species (Aitchison 1984), no *Pardosa* species were found to overwinter in adult stage.

For this experiment we chose two common *Pardosa* species: *Pardosa agrestis* (Westring 1861) and *Pardosa hortensis* (Thorell 1872). There is a clear difference in the habitat preference of the two species. Although both of them can be found together in most of the

agricultural habitats in Hungary, *P. hortensis* can reach extreme dominance among cursorial spiders in gardens and grass-covered vineyards (Kiss pers. obs.), while *P. agrestis* is by far the most abundant spider species in arable fields (Samu et al. 1996; Tóth 1999). The two species have different phenological patterns in Hungary. *Pardosa hortensis* has one reproductive period in spring (in April–May), while *P. agrestis* adults have two separate peaks a year (in May–June and in August) (Samu et al. 1998; Samu & Szinetár in press).

Since adult individuals in the genus *Pardosa* seem to be unable to overwinter, the regulation of the autumnal development of immature individuals is of pronounced importance to avoid untimely maturation before winter, especially in geographical areas with unpredictable warm periods in autumn. In contrast with the numerous publications on life history patterns of *Pardosa* spp., surprisingly few manipulative studies have investigated the factors determining their pre-overwintering development. In his comprehensive study Schaefer (1977) assumes that in spiders,

similar to insects, photoperiod and temperature are the principle factors in the evocation and termination of the dormancy. In the sporadic studies on the dormancy phenomenon in spiders two types of dormancy, quiescence and diapause, are generally distinguished. Quiescence is a simple retardation of development due to the unfavorable level of some physical factor (e.g. temperature), which can be resumed without delay by favorable changing of that factor. In contrast with quiescence, the state of diapause imply basic changes in the hormonal status of the spider, thus diapause cannot be immediately released by favorable changing of the inducing environmental factor (Schaefer 1977). In some stenochronous species reproducing in spring and summer, low temperatures as well as short daylengths were shown to retard the development of immature individuals. The mechanism of this retardation can be the prolongation of intermolt cycles and, in some cases, the increasing of the number of instars (Schaefer 1976). Miyashita (1969) found a strong inhibition of molting in penultimate instars of *Pardosa astrigera* L. Koch 1878 collected at the beginning of the overwintering season from the field. The inhibition was persistent even in warm conditions with long day length. Schaefer (1987) has shown that penultimate instars of the wolf spider *Pirata piraticus* (Clerck 1757) overwinter in diapause, while younger juvenile stages in quiescence. In the present study we tested how different temperature and daylength affects the development of the pre-overwintering individuals of two common *Pardosa* species having different phenological patterns.

METHODS

Immature *Pardosa agrestis* and *P. hortensis* individuals were collected respectively from an alfalfa field dominated by *P. agrestis* on 30 September 1998 and from an abandoned garden dominated by *P. hortensis* on 10 October 1999, near Budapest (Hungary). Spiders were collected individually regardless of their size, thus representing the approximate size distribution of the population on the site at the date of collection. The spiders were placed in separate plastic vials (diameter = 3 cm; height = 6 cm) with moistened plaster of Paris on the bottom. The vials with spiders were randomly assigned to one of four light boxes represent-

ing either of the four treatments arising from two temperature groups (outdoor/indoor) and two levels of light regime (light:dark 16:8 and 8:16). All the four treatment groups of *P. hortensis*, and the two outdoor temperature groups of *P. agrestis* started with 50 animals, while in the case of *P. agrestis* the two indoor temperature groups started with 75 spiders. The light boxes ensured a free air flow from the outside, thus the temperature within the boxes was the ambient temperature (indoor or outdoor) hourly recorded by data loggers. The light was provided by neon gas lighting tubes controlled by timer switch for each box. The tubes were isolated by a transparent glass from the inside space of the boxes to avoid light dependent heating effect. The two boxes of the outdoor temperature groups were placed inside a chicken wire sided garden-shed, thus the temperature followed natural-like daily curves. The boxes of the indoor temperature groups were placed in a room with controlled temperature. To ensure a daily temperature rhythm, the constant 26 °C temperature was lessened to 18 °C for 4 h each day in the middle of the dark period. The cooling procedure took ca. 30 min, while 5 min were needed to reach the 26 °C again. The spiders received fruit flies (*Drosophila melanogaster*) *ad libitum*. Checks for molting took place three times a week. The experiments ended on 1 March both years.

Two statistical methods, Gehan's Wilcoxon test (Gehan 1965) and proportional hazard (Cox) regression (Cox 1972), offered by the Survival and Failure Time Analysis module of the Statistica program package (Statsoft, Inc. 2000) were used to compare the tendency to molt and the tendency to reach adulthood of the spiders under different conditions. The main advantage of these methods, as compared to more generally used statistics, is that "censored" cases, in which we only know that the event in question did not occur before a given time, e.g. the experimental individual did not molt before the end of the experiment or before its death, can be analyzed together with "complete" cases, in which the event was actually observed and thus the complete time to the occurrence of the event was known. An other important point is that neither of the two methods have constrains concerning the distribution pattern of the underlying time periods.

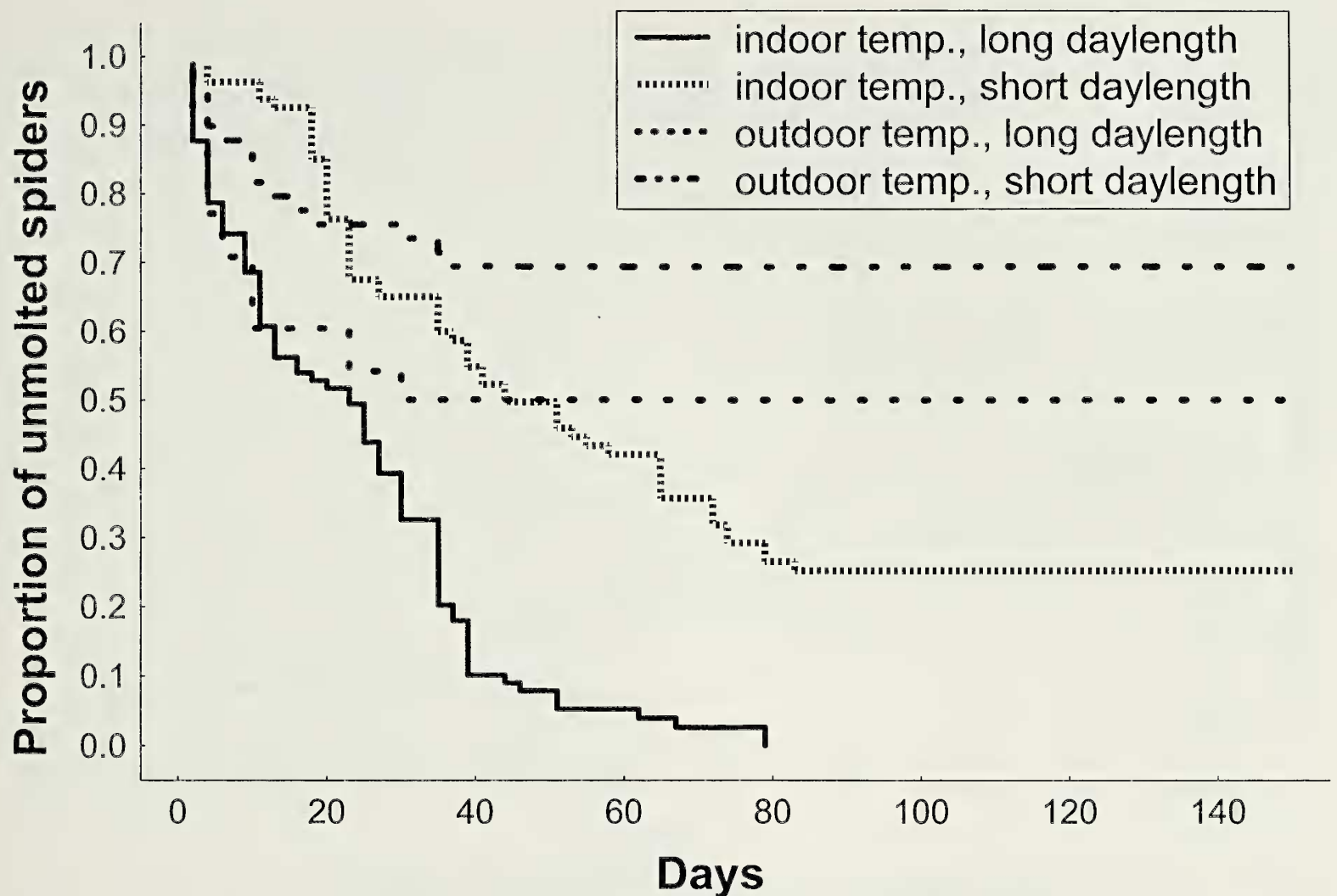


Figure 1.—Proportion of unmolted *Pardosa agrestis* individuals changing with time over the course of the experiment in the four treatments.

RESULTS

Outdoor temperature groups.—In the case of *P. hortensis* none of the immature spiders molted during the experiment, irrespective of the light regime. In *P. agrestis* 24 and 15 individuals molted at long and at short daylength respectively, the spiders molted significantly sooner at long than at short daylength (Gehan's Wilcoxon test: $Z = -2.15$, $P = 0.031$). No individuals molted more than once, and none of them became adult. The molting events ceased after 5 November, as the daily maximum temperature decreased and no longer reached 10 °C (Fig. 1). In the autumnal months only four experimental spiders were lost (1 *P. hortensis* and 3 *P. agrestis*), while during the winter months (December–February) the mortality rates were high (60 % in *P. hortensis* and 76 % in *P. agrestis*).

Indoor temperature groups.—*Pardosa hortensis*: No immature *P. hortensis* was left by the end of the experiment. Ninety-one individuals reached adulthood within 90 d, 86 of them in one, five of them in two molts. Nine of the 100 experimental spiders died be-

fore maturing. The first molting to adulthood occurred 17 d after the beginning of the experiment. The average time to reach adulthood was significantly longer at short day length (mean \pm SD: 64 ± 17.2 days) than at long day length (36 ± 15.1) (Mann-Whitney U test: $Z = -6.25$, $P < 0.001$). The proportion of males ($n = 49$) and females ($n = 42$) in the experimental animals did not differ significantly from 50%. In the regression model containing light treatment and gender as predictor factors gender had no significant influence on the time needed to reach adulthood (Proportional hazard (Cox) regression: $\chi^2 = 28.41$, $df = 2$, $P < 0.001$; effect of light regime: $t = -5.29$, $\beta = -1.27$, $P < 0.001$; effect of gender: $t = 1.14$, $\beta = 0.12$, $P = 0.255$) (Fig. 2).

Pardosa agrestis: Seven and 19 immature spiders were lost (died or escaped) before the end of the experiment at long and short daylength respectively. All of the surviving individuals became adults at long daylength ($n = 68$), while at short daylength 42 of the 56 spiders molted at least once, and 38 of them

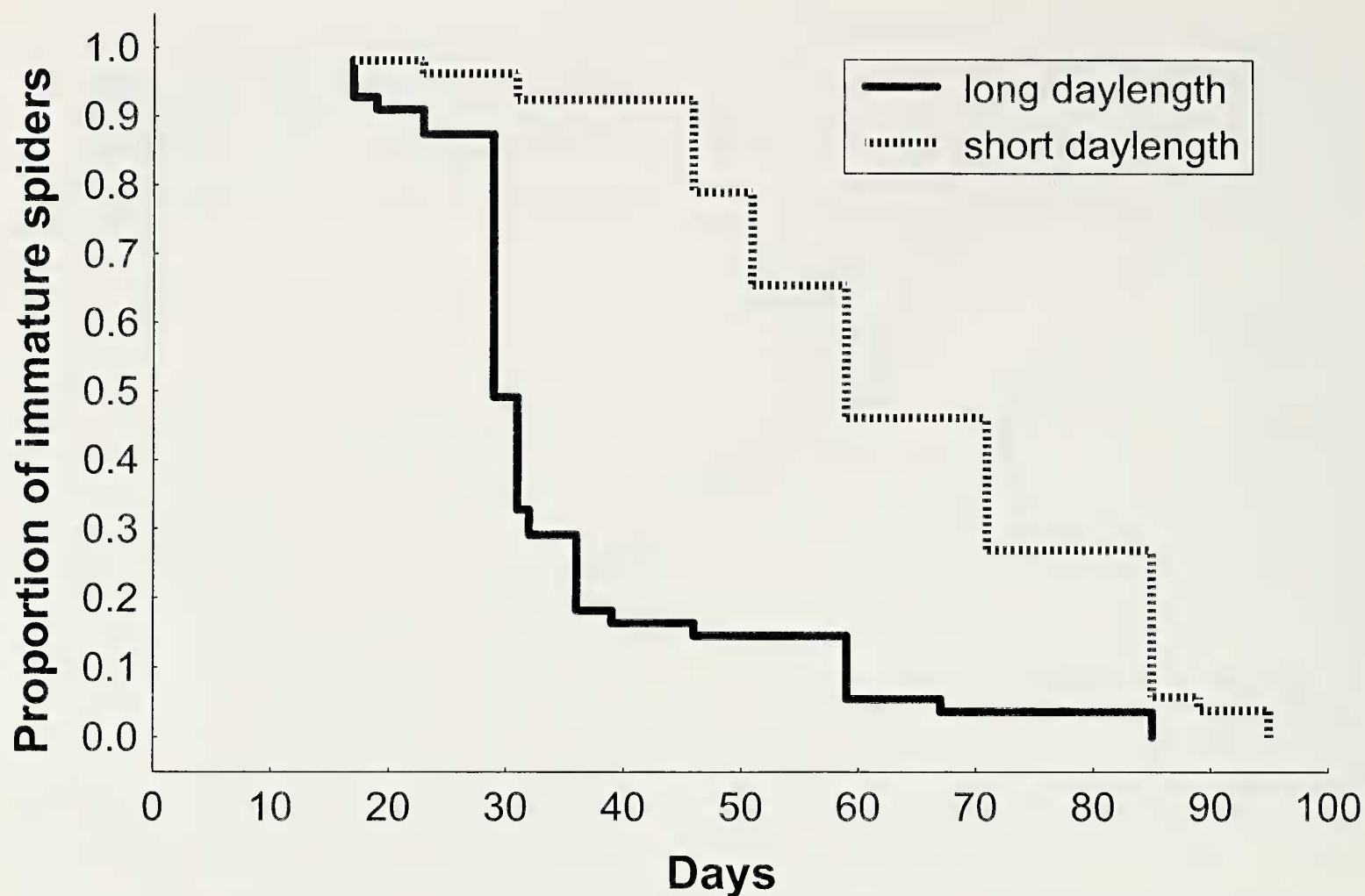


Figure 2.—Proportion of immature *Pardosa hortensis* individuals changing with time over the course of the experiment under different light regimes at indoor temperature.

reached adulthood. One to four molts were needed to reach adulthood ($n = 15; 53; 31; 7$); the distribution of the number of molts needed did not differ significantly between the light regimes (Correspondence analysis $\chi^2 = 0.19$, $df = 3$, $P = 0.979$). In the adults, the proportion of males ($n = 50$) and females ($n = 56$) did not differ significantly from 50%. The time to reach adulthood at short daylength (mean \pm SD: 84 ± 17.1 d) and at long daylength (55 ± 31.5 d) naturally depended on the number of molts needed, but more importantly it significantly depended on the light regime, but not on gender (Proportional hazard (Cox) regression: $\chi^2 = 26.53$, $df = 3$, $P < 0.001$; effect of light regime: $t = -3.43$, $\beta = -0.76$, $P < 0.001$; effect of number of molts: $t = -3.95$, $\beta = -0.55$, $P < 0.001$; effect of gender: $t = -0.79$, $\beta = 0.16$, $P = 0.431$).

The length of the time to the first molt after getting into the laboratory was significantly influenced by the number of the further molts needed to reach adulthood and the light regime. Individuals of earlier stages molted sooner than later instars; spiders molted sooner at long than at short daylength (Proportion-

al hazard (Cox) regression: $\chi^2 = 68.92$, $df = 2$, $P < 0.001$ effect of light regime: $t = -7.12$, $\beta = -1.32$, $P < 0.001$; effect of number of further molts prior to adulthood: $t = 5.27$, $\beta = 0.86$, $P < 0.001$). In the case of the individuals collected as penultimate instars, the average time to their first and final molt was 41 ± 11 d ($n = 10$) and 65 ± 26.9 d ($n = 5$) under long and short daylength conditions, respectively. The minimum time to the first molt in penultimate instars was 18 d. We did not observe this type of threshold in the individuals of the three earlier stages, in which molts occurred from the first day of the experiment (Fig. 3).

In contrast to the lengths of time to first molt in the laboratory, which represent only a fragment of a complete intermolt period, the lengths of further intermolt periods, which were completely accomplished in the laboratory, did not depend significantly on either developmental status, or on light regime (Proportional hazard (Cox) regression: $\chi^2 = 3.64$, $df = 2$, $P = 0.16$ effect of light regime: $t = -0.84$, $\beta = -0.14$, $P = 0.40$; effect of number of further molts prior to adulthood: $t = -1.64$,

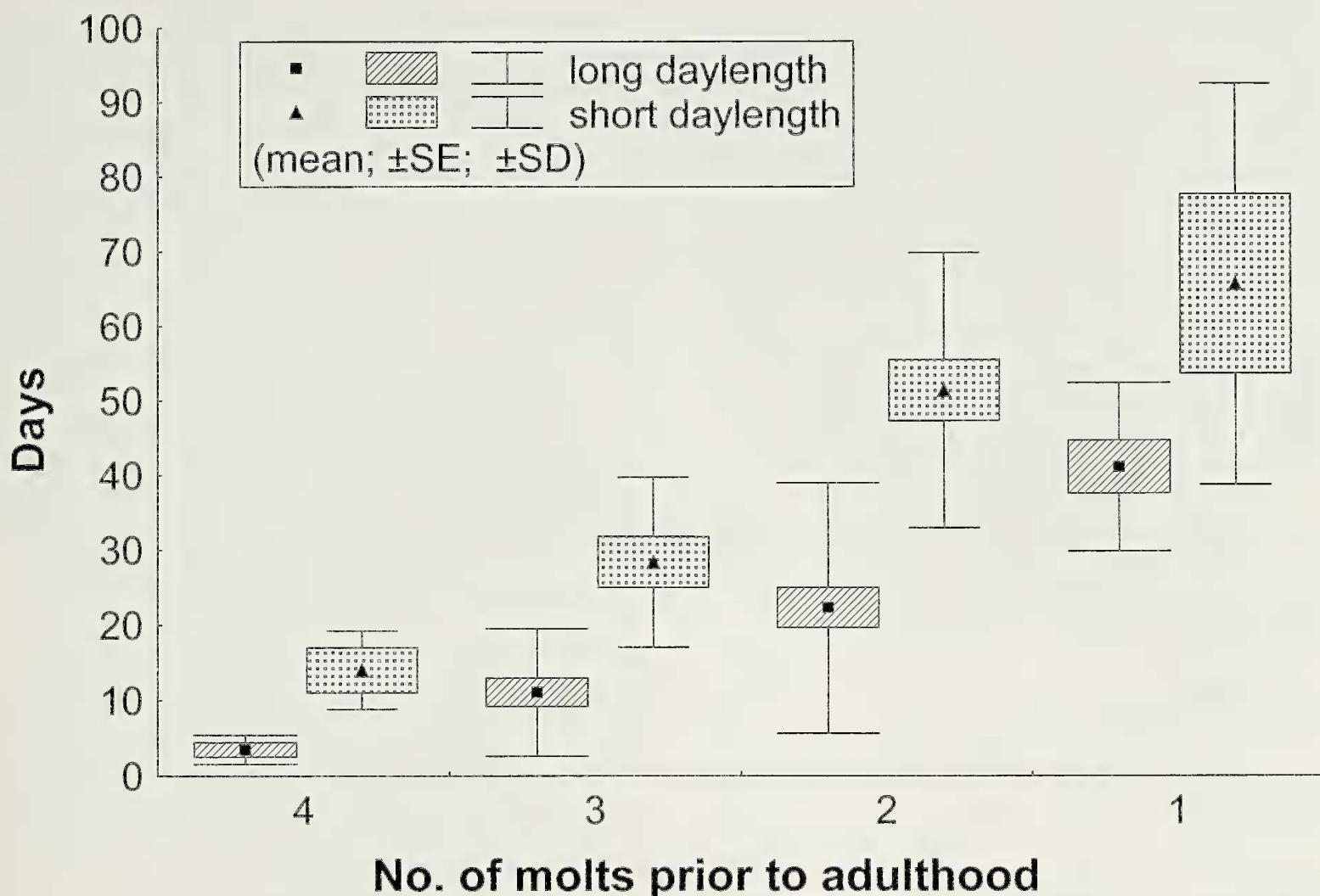


Figure 3.—Length of time to first molt from the beginning of the experiment in different developmental stages of *Pardosa agrestis* under different light regimes at indoor temperature.

$\beta = -0.28$, $P = 0.10$) (Fig. 4). Thus, differences in the time to reach adulthood were completely due to differences in the time to the first molt in the laboratory.

DISCUSSION

The results that no *Pardosa* individuals molted to adulthood at outdoor temperature, and that *P. agrestis* had a more heterogeneous stage distribution than *P. hortensis* are in accordance with our previous knowledge about the phenology of the two species (Samu et al. 1998; Samu & Szinetár in press). In contrast with the field results of Tóth et al (1997), who found that adults of *P. agrestis* males appear somewhat sooner than females in the field, under the present laboratory conditions male and female maturation times did not differ significantly from each other.

The overwhelming importance of temperature on the development rate of spiders is well known (Schaefer 1987). Our results suggest, that a clear distinction has to be made between penultimate instars and earlier juvenile stages considering the regulation of pre-overwinter-

ing development. The development of penultimate instars was halted at outdoor ambient temperatures in autumn and even the treatment of warm temperature regime with long daylength needed a considerable time to release this stasis. In contrast, the development of earlier stages of *P. agrestis* was only arrested by the relatively low autumnal outdoor temperatures and individuals in the indoor temperature groups benefited immediately from the advantageous conditions. Similar difference in the pre-overwintering development between penultimate instars and earlier juvenile stages of the same species was also reported by Schaefer (1987) in *Pirata piraticus*.

In agreement with the studies demonstrating that for a number of stenochronous species short daylength increases the lengths of the intermolt periods (Schaefer 1987), in the present study short daylength conditions decreased the tendency to molt in both species and all stages. On the other hand, short daylength was not shown to increase the number of instars in *P. agrestis*. It is rather difficult to interpret why light regime and development

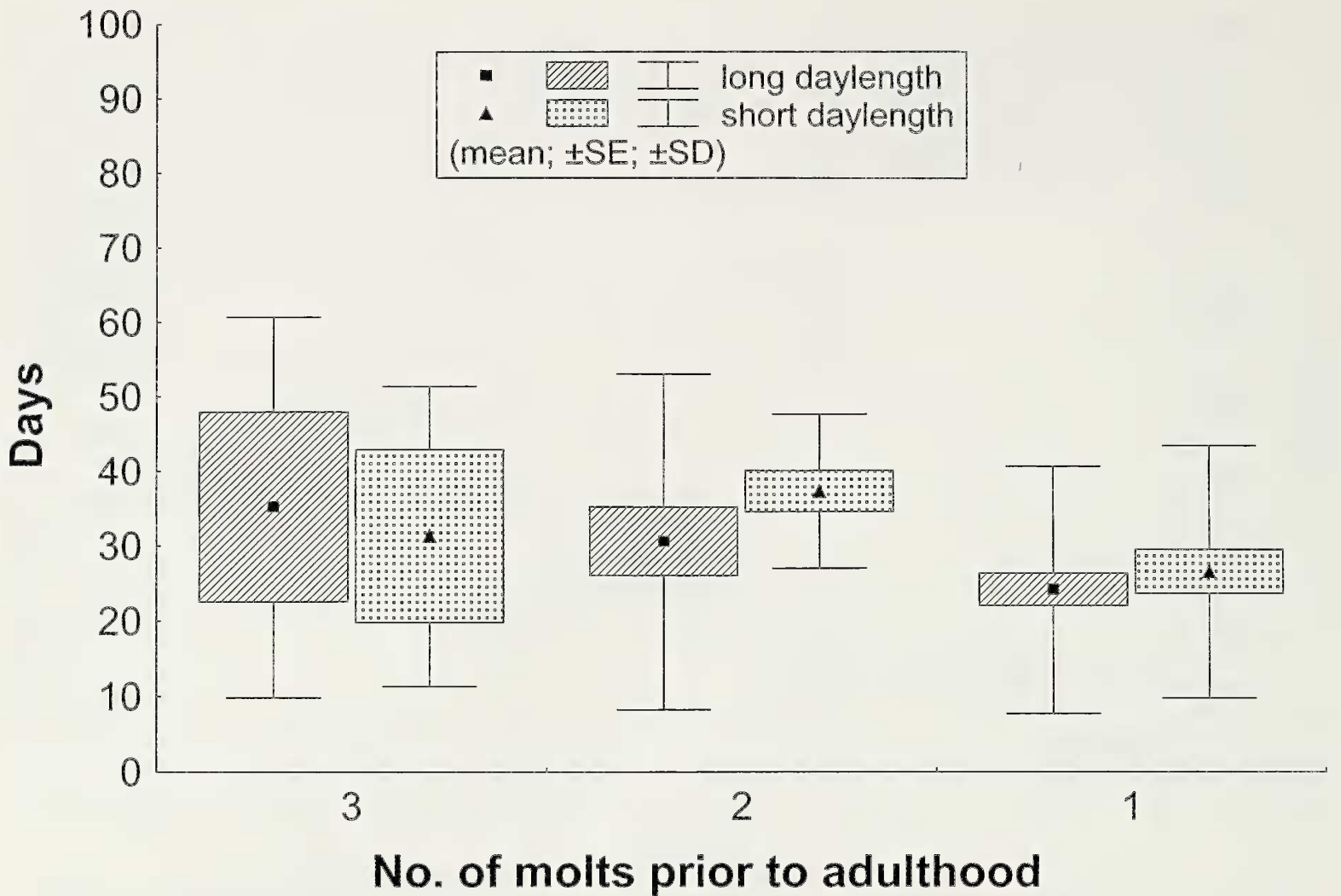


Figure 4.—Length of the intermolt periods completely accomplished in the laboratory in different developmental stages of *Pardosa agrestis* under different light regimes at indoor temperature.

stages affected only the time to the first molt in laboratory significantly, and not the further intermolt periods. We can assume that the regulation of the molting cycles and the diapause in spider species overwintering exclusively as immature instars is based on similar hormonal mechanism in different species. Bonaric (1987) found low levels of molting hormones (ecdysteroids) in the overwintering instars of *Pisaura mirabilis* (Clerck 1757) and demonstrated that the sensitivity of the overwintering instars to injected exogenous ecdysteroids increased throughout the overwintering period. This latest result can be interpreted as a possible inhibition of the effects of molting hormones at the beginning of the overwintering. Our results suggest that in *Pardosa agrestis* an inhibition of molting is increasingly present in the more developed instars in the pre-overwintering season. Once the inhibition was surmounted by artificial conditions, the molting cycles were no longer inhibited and did not depend anymore on developmental stage or light duration.

The dichotomy of the strong inhibition in autumn to reach adulthood in penultimate in-

stars, and the readiness to molt as long as favorable temperature conditions occur in earlier stages, might be a general rule in the pre-overwintering development of Holarctic stenochronous wolf spiders with spring-summer reproduction. This phenomenon certainly has a synchronizing effect on the stage composition of populations. However, this effect depends on the life history pattern of the species. In populations in which the majority of the individuals reach the penultimate stage relatively soon, individuals can compensate even considerable time-lags in their development and thus most of the individuals overwinter as penultimate instars. This is the case in *Pardosa hortensis* in Hungary in which, as a consequence, a very strict stenochrony can be observed in the appearance of adult stages at the beginning of April (Kiss pers. obs.). On the other hand, in later maturing populations in which the individuals are mostly in earlier developmental stages in autumn, the proportion of the instars reaching the penultimate stage before overwintering is highly variable year to year, depending on weather conditions. This yearly variation in the synchronization of

developmental stages in autumn may lead to different phenological patterns in different years, as it is reported for *P. agrestis* in Hungary (Samu et al. 1998).

In summary we can conclude that the pre-overwintering development of both studied species was shown to be controlled by autumnal temperature and daylength. Temperature and daylength act primarily to prevent the precocious maturation of penultimate instars. This study showed additionally that the strength of this control was stage dependent. The stronger inhibition of molting in later instars contributes differently to the stenochrony of species with different phenological pattern.

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